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17. Buprestoidea Crowson, 1955

Charles L. Bellamy & Mark G. Volkovitsh

The superfamily Buprestoidea was established by Crowson (1955) for the family Buprestidae Leach, 1815, which differs from other members of the Elateriformia by the combination of: head, hypognathous; antennae, mostly serrate; transverse suture of metaventrite, present; and basal two abdominal sterna: connate. The fundamental questions in the study of the superfamily are 1) whether there should be one or more families considered, and 2) if the tribe Trachyini (Agrilinae) is monophyletic? Two more fundamental questions are: what is the sister group for Buprestoidea, and how many subfamilies of Buprestidae should be recognized and what are their relations?

The Schizopodidae LeConte, 1859, have been contested at both the family and subfamily levels, however from a strict phylogenetic perspective, until a sister-group is established, familial status will remain contentious. The group was most recently considered at the family level by Nelson & Bellamy (1991) and subsequently supported by Kolibáč (2001), Nelson & Bellamy (2002), and Bellamy (2003). However, Hołyński (1993), Lawrence & Newton (1995) and Volkovitsh (2001) chose to retain it at the subfamily level. Until the sister-group of Buprestidae/Buprestoidea is established, this debate will remain unresolved. For the purpose of this discussion, we will outline morphological features that distinguish them from the other main buprestid lineages.

The higher classification is in an active flux and what will be summarized herein represents a contemporary synthesis of the most recent proposals, at least in the most parsimonious outline we can present. Seven subfamilies, if Schizopodidae is considered at that level, are used now to contain 50 tribes and 472 genera. The total number of valid species is somewhat above 14600. A complete summary of buprestoid higher classification is by Bellamy (2003).

17.1. Buprestidae Leach, 1815

Distribution. In general, buprestids are known from almost every terrestrial habitat on earth. Wood-boring species abound in temperate and subtropical habitats, while leaf- and stem-mining species are the most diverse in the humid tropics, due to the higher degree of fungal attack on dead-wood inhabitants in rainforest habitats.

Biology and Ecology. In the strictest sense, buprestids are wood-borers as larvae (Fig. 17.1.4), but in some lineages they have evolved into stem- or root-borers or leaf-miners. In arid and semi-arid habitats, the wood-boring habit has required that many species utilize the woody roots of perennial shrubs. Some groups, likely of independent origin, are free-living, soil-dwelling, external root feeders, e. g., Schizopodidae (Fig. 17.1.3) and Julodinae. Eggs are deposited in cracks or scars in the bark, or exposed wood, on or near the root-crown or directly on or in the plant tissue and the larvae chew their way into the substrate. For those species whose larvae feed in roots, the female will oviposit below the soil adjacent to the root. Females of external root feeders drop their eggs on the soil at the base of the host plants.

Adults feed on: 1) foliage of the larval host plant; 2) foliage of other plants; or 3) visit flowers to feed on pollen and nectar. Flower-visiting species are likely to be at least secondary pollinators, especially those species that can transmit pollen from either the body vestiture (e. g., Polycestinae: Acmaeoderini) or those with mouthparts strictly adapted to nectar feeding (e. g., Buprestinae: Stigmoderini).

Morphology, Adults (Figs. 17.1.1, 17.1.2). In general, shape nearly cylindrical to flattened, elongate-ovoid, transversely convex above and below, or cuneiform; size 2 to 75 mm or more in length, usually less than 20 mm; color various, often metallic with bright iridescent reflections, or dark-colored with patterned or irregular pigmented maculae as spots, fasciae or vittae; vestiture absent or variously covered with setae and sometimes broad scale-like setae.

Head deflected, resting on the prosternum, retracted into the prothorax, but mostly as broad as the anterior portion of pronotum; surface punctate or rugose punctate. Antennae usually with 11 antennomeres (exceptions are e. g., *Acmaeoderella* s.g. *Kocheridia*, *Micropistus*, *Philocteanus* – 10, Dystaxiini, *Hypostigmodera* – 12), usually serrate, in some males flabellate or pectinate; inserted some distance from the eyes and mandibles, on the front within distinct frontoclypeal cavities; disposition and orientation of an-

Fig. 17.1.1. Adults, habitus. A, *Dystaxia elegans* (Schizopodinae); B, *Agrilus cavifrons* (Agrilinae); C, *Temognatha pictipes* (Buprestinae); D, *Julodis viridipes* (Julodinae); E, *Asymades transvalensis* (Agrilinae); F, *Steraspis ambigua* (Chalcophorinae).

tennal sensory organs and sensillae variable (see Volkovitsh 2001). Anteclypeus sometimes visible, labrum small, distinct, often bilobed and setose distally; mandibles small, stout basally, curved, the apices acute; maxillary palpi with four palpomeres, filiform; mentum quadrate to triangular; ligula usually not prominent; labial palpi with three palpomeres, filiform. Eyes lateral, moderate to large, greatly elongate-oval to reniform, inner margins sometimes strongly converging, upper margins in some males of *Coomaniella* contiguous.

Pronotum slightly broader than the head; shape irregularly quadrate, sometimes narrowed in front; lateral margins usually carinate, carinae sometimes incomplete from lateroposterior angle; surface punctulate to strongly rugose, sometimes with elevated relief areas or/and deep depressions; hypomeron generally broad; prosternum long and broad, produced as a process posteriorly between the coxae and inserted into either a cavity of the mesoventrite or a cavity comprised of the short lobes of the mesoventrite laterally and the metaventrite distally. Metaventrite usually with the vestige of a transverse suture near the posterior coxal plates. Legs with the trochantins of the fore- and middle-legs exposed; anterior coxae small, oval, not contiguous, procoxal cavities open behind; middle coxae small, flat, almost quadrate, separate; hind coxae large, transverse, with thick plates; trochanters small, triangular; femora subparallel to fusiform; tibiae slender, sometimes dentate or spinose, the apical spurs moderate; tarsal formula 5-5-5, tarsi slender, at least some preapical tarsomeres bilobed, distal tarsomeres with ventral pulvilli; claws simple, appendiculate or bifid, sometimes asymmetrical, rarely sexually dimorphic. Scutellum trapezoid, triangular to cordifrom, moderate to small; sometimes hidden beneath elytral base or completely reduced (Acmaeoderina).

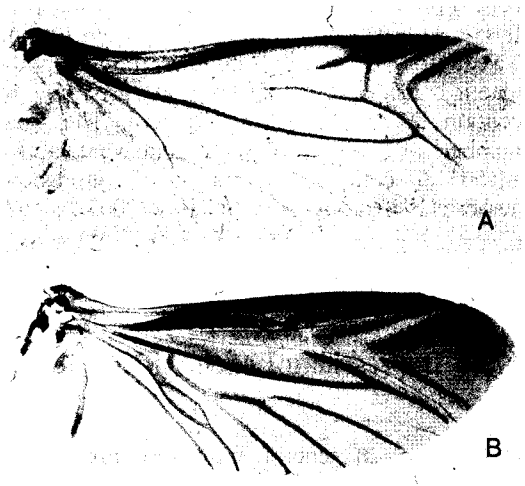

Fig. 17.1.2. Hind wings. A, *Dystaxia elegans*. B. *Mendizabalia germaini*.

Elytra mostly entire, apically rounded or acuminate and often with one or more apical spines, rarely exposing more than pygidial tergite except in rare cases, e. g., *Curis splendens* Macleay (Australia), *Hesperorhipis* spp. (Southwest North America); striae punctate or carinate; intervals smooth, punctate or rugose; margins, especially apical portion serrate to serrulate, or seldom glabrous or with paired or several apical spines; epipleural fold indistinctly separate or with fine carina separating it from disc, broad basally. Wing venation and folding (Fig. 17.1.2.; see Forbes 1922, 1926, 1942 a, 1942 b; Good 1925; Kukalová-Peck & Lawrence 1993): with 2 A with three branches; wedge cell, when present, acute apically with only one vein coming from it. Folding pattern of the wing with area A and B normally reduced to slender crumples, area C about half the length of the wing, frequently fused more or less completely with area D which is either open to the costa or reduced to a slender crumple; area H always well marked and reaching the margin for the full width, very slender and nearly longitudinal in the more typical forms; commonly with one chevron-like apical fold, but may be two, or absent; anal lobe highly variable, but never free.

Abdomen (see Jendek 2001) with five visible sterna, the first and second connate; sutures shallow, sometimes partly obsolete laterally; terga I and II connate; dorsal and ventral sides with paired pore-like areas (cuticularia, Jendek 2001); lateral sternal projections extending up to the anterior margin of tergite I; surface smooth, punctate, or rugose. Reproductive system and genitalia see Gardner (1989). Male genitalia of a modified trilobed type unique for Buprestidae; the penis (median lobe) usually comprises two flat, dorsal and ventral plates, nearly parallel-sided basally, the apex acute to transverse, grooved deeply on ventral side, internally with ejaculatory duct and internal sac, bearing spines, denticles, scales, etc.; parameres sometimes highly modified from swollen to having projecting membranous lateral lobes and sensory setae distally, parameres surround most of the penis (median lobe), fused to the pars basalis (basal piece); pars basalis fused, forming a basal plate. Female genitalia generally with the valvifers reduced to a large, strong baculum; coxite dorsally with a baculum, the membranous part expanded preapically; stylus greatly reduced, proctiger large with two bacilli which extend around to the ventral surface where they meet and articulate with the basal parts of the valvifers.

Exceptions and variation. Schizopodidae: can be distinguished by the wide metathoracic anepisternum and deeply bilobed fourth tarsomere. They possess a primitive wing venation (Forbes 1942 a), compared to buprestids in general, and yet the genital structures of both sexes are highly derived (see Gardner 1989; Nelson & Bellamy 1991, 2002). The body of schizopodids is somewhat to very stout and strongly convex; they vary in size with the length 6.2 mm to 18.0 mm. The surface sculpture varies from coarse in Schizopodini to smooth and finely punctate in Dystaxiini.

Head with frons flat or slightly convex; eyes feebly emarginate near mid-point of anterior margin. Antennae with sensillae partly diffuse on both surfaces and partly concentrated in apical depression (Schizopodini) or lateral foveae (Dystaxiini); in Schizopodini with 11 antennomeres, each thick and transversely triangular, sensory pores diffuse on both surfaces; in Dystaxiini, with 12 antennomeres, flattened and elongate triangular with sensory pores partially concentrated in fovea. Thorax roundly trapezoidal; mesoventrite forming cavity for prosternal process; metathoracic anepisternum wide; femora unarmed; tarsi with five tarsomeres, fourth deeply bilobed. Abdomen: female with five entire, visible sterna, male with six sterna, 5 and 6 deeply emarginate; male aedeagus with basal piece and parameres fused into an asymmetrical tubular tegmen, penis (median lobe) also asymmetrical; female genitalia with relatively short paraprocts and valvifers and with sclerotized coxites plate-like. The metathoracic wings are characterized by media extending basally, the radial cell situated more apically, and the radiomedial cross-vein much longer than is characteristic of the Buprestidae. The wings also have a normal hinge system at the end of the radial cell that is lacking in even the most complexly folded buprestid wings.

Julodinae: mostly medium to large bodied, with the head strongly deflected, mostly invisible from above; antennomeres densely covered with modified sensillae with inconspicuous sensory organs; bodies very robust and nearly cylindrical in cross-section, tapering strongly to posterior aspect of elytral/abdominal terminus; tarsomeres with large, broad ventral pulvilli; female ovipositor very stout, sclerotized. Bodies often with small to large depressions, foveae or depressed vittae, filled with dense setae in various colours, or with projecting tufts of setae in some southern African species of *Julodis* Eschscholtz, 1829.

Polycestinae: cavity for reception of prosternal projection formed entirely, or mostly, by lobes of mesoventrite; body often punctured strongly or elytra carinate; male parameres without setal groups apically.

Galbellinae: mostly small, similar in appearance to some leaf-mining genera, e. g., *Pachyschelus*, and having deep hypomeral grooves for reception of antennae in repose and with the

femora expanded and explanate to hide tibiae and tarsi.

Chalcophorinae: mostly large beetles, with tarsomeres 1–4 often with ventral pulvilli similar to tarsi of julodines; antennomeres with the sensory pores mostly diffuse over both upper and lower surfaces, sometimes confluent in the big apical or/and lateral foveae; fresh specimens often covered with secreted waxy pulverulence.

Buprestinae: generally smaller, mostly with only distal tarsomeres with ventral pulvilli; antennomeres with sensilla usually partially submerged, concentrated in pits, foveae, or open or closed cavities, and, partly, in lateral fields.

Agrilinae: smaller yet, the most diverse group, containing the largest genus *Agrilus* Curtis, 1825 (ca. 2700 described species); the tribe Coraebini the most diverse at the genus level; leaf-mining taxa in apparently polyphyletic Trachyini not necessarily placed correctly.

Morphology, Larvae (Figs. 17.1.3, 17.1.4). Known as flat-headed wood borers; body long, slender, subcylindrical, or enlarged, segments flattened, or oval, deeply notched and tapering posteriorly; club-like head and thorax may or may not be enlarged (leaf-miners); rarely with the mid-abdominal segments the widest, length 5 to 80 mm or more; vestiture usually absent; color cream to near white, sometimes with yellow, orange, or brown pigmented spots. Head small, depressed, more or less retracted into the prothorax. Antennae 2- or 3-segmented with big cone-like sensory appendage. Labrum arcuate, free; mandibles stout, toothed, spoon-shaped; maxillae with two-segmented palpi and a lobe-like mala; labium small, with ligula prominent, spatulate; labial palpi small, one-segmented, or absent. Stemmata frequently absent. Thorax without legs, sometimes with vestiges; prothorax dorsally with a distinct single, double, 'Y'-, or 'V'-shaped groove or sclerotized plates (some Trachyini), ventrally with a single groove; Schizopodinae and Julodini have no distinct groove on both sides. Abdomen usually ten-segmented, often with two fleshy lobes apically; sometimes with tenth segment terminating with a pair of sharp, sclerotized, toothed fork- or forcep-like fixed urogomphi laterally. The spiracles are cribriform, usually crescent-shaped, on the mesothorax and abdominal segments I to VIII. The only keys to larvae are those by Cobos (1986) for world wide higher taxa, Bílý (1999) for Europe, and Burke (1917) for North America.

Exceptions and variation. Schizopodinae (Fig. 17.1.3): known (*Schizopus*: Rees 1941), or putative (*Dystaxia*? sp.: Lawrence 1991: p. 388, Fig. 34.394); larvae have a cylindrical body, nearly parallel laterally; head with three well-developed unequal stemmata on each side posterior to and slightly dorsal to antennal base; thoracic segments legless; abdominal segments I–VIII each with a pair of well-developed pro-legs terminating in hoof-shaped structures; mesothoracic, metathoracic, and abdominal segments I–VII each with a pair of ventral glands, each with a protracted duct. Spiracles biforous.

Julodinae: Larvae of *Julodis* species have been described by Bílý (1983) and Lesne (1898). First instar of *Sternocera* with moderate covering of long, stout setae to protect from soil abrasion; final instar with only sparse covering of short, fine setae. The mandibles are strongly modified, e. g., with wide, shovel-shaped vertical lamina, as are other features of the mouthparts, such as the articulating labium and the well-developed hypopharynx. Spiracles modified multiforous buprestoid type.

Polycestinae (see also Bílý 1986, 1989, 2000; Volkovitsh & Hawkeswood 1999): a single groove on the thoracic shield quickly distinguishes polycestine larvae from the more typical buprestid larvae found in wood. Another polycestine feature is an additional projection of uncertain origin on the maxillary stipes (except for known Australian genera). Spiracles uniforous to multiforous buprestoid type.

Galbellinae: the larvae of two species of *Galbella* were recently described by Volkovitsh & Bílý (2001) which showed the relationship of this group to be with the "primitive" end of the family line rather than with the leaf-miners where they had been placed traditionally. These larvae are similar to the polycestines sharing the single pronotal groove. Spiracles uniforous to multiforous buprestoid type.

Chalcophorinae (see also Bílý & Volkovitsh 1996, 2001): larvae of Chalcophorini *sensu lato* (including known Chrysochroini, Hypoprasini) are very typical and differ mostly from those of the Buprestinae by having the pronotal and prosternal plates well-developed, oval-shaped, with 'Y'-shaped pronotal groove, and with fields of sclerotized, irregular asterisk-like or transverse asperities; those of psilopterine taxa bear grain-like asperities bordering the prothoracic grooves; some taxa (Paratassini, *Nanularia*, Poecilonotini) have no asperities on the prothoracic plates, which are partly or completely covered with microteeth. Spiracles of multiforous buprestoid type.

Buprestinae: Most diverse group concerning larval characters. Pronotal groove usually 'V'-shaped; prothoracic plates glabrous (many Anthaxiini, Anilarini, Kisanthobiini), covered with microteeth with areas of grain-like asperities (Buprestini), completely covered with regular grain-like or slightly transverse asperities (Melanophilini, Chrysobothrini), sometimes bearing big transverse asperities like those in Chalcophorini along the grooves (some *Melobasis*, *Cylin-*

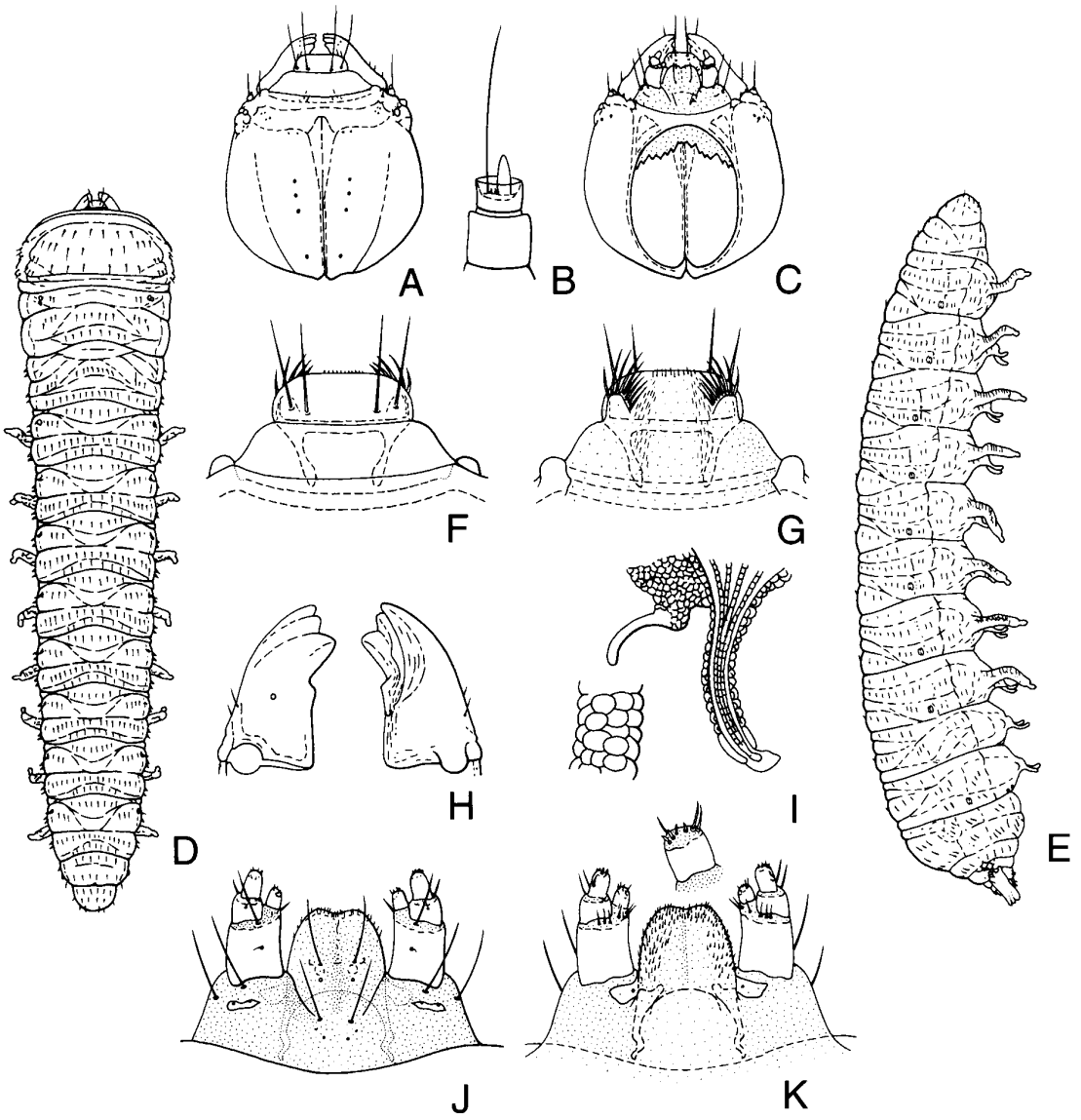

Fig. 17.1.3. Larva of *Schizopus*. A, head, dorsal view; B, antenna; C, head, ventral view; D, habitus, dorsal view; E, habitus, lateral view; F, clypeus and labrum; G, epipharynx; H, mandible; I, J, K, maxillae and labiohypopharyngeal complex, ventral and dorsal view. (redrawn, from Rees 1941).

drophora). Spiracles of multiforous buprestoid type. (See also Volkovitsh & Hawkeswood 1987, 1993, 1995; Bílý & Volkovitsh 2001).

Agrilinae: Abdomen sometimes with segment X terminating with a pair of sharp, sclerotized, toothed fork- or forcep-like urogomphi laterally. As far as have been investigated, the larvae of this subfamily lack the proventriculus of the alimentary canal. Pronotal plate with single longitudinal, double or 'Y'-shaped groove, trachyine taxa frequently with sclerotized plates. Antennal sensory appendage never retracted; mandibles with setal brushes on inner margin. Spiracles of peculiar agriloid type, with abdominal spiracles in some trachine taxa resembling uniforous type. (See also Bílý 1986, 1993, 1997; Volkovitsh & Hawkeswood 1990).

Morphology, Pupae (Fig. 17.1.4 R). Exarate, in all known cases. Pupae of wood-boring larval species live in chambers at the terminus of tunnels, just beneath a thin layer of bark or wood that will be chewed through by emergent imago or with exit holes plugged with wood or bark material. Pupae of external root feeding larval species transform in protective earthen cell. Pupae of leaf-mining species vary in the construction of the pupal case, which supports the opinion that the Trachyiini might be a paraphyletic assemblage of taxa. Sometimes the pupae are naked (Brachyina: *Brachys*, *Taphrocerus*), sometimes enclosed in a frass pupal case (Leiopleurina: *Leiopleura*) or sometimes in a woven ("silk"?) pupal case (Pachyschelina: *Pachyschelus*, *Hylaeogena*).

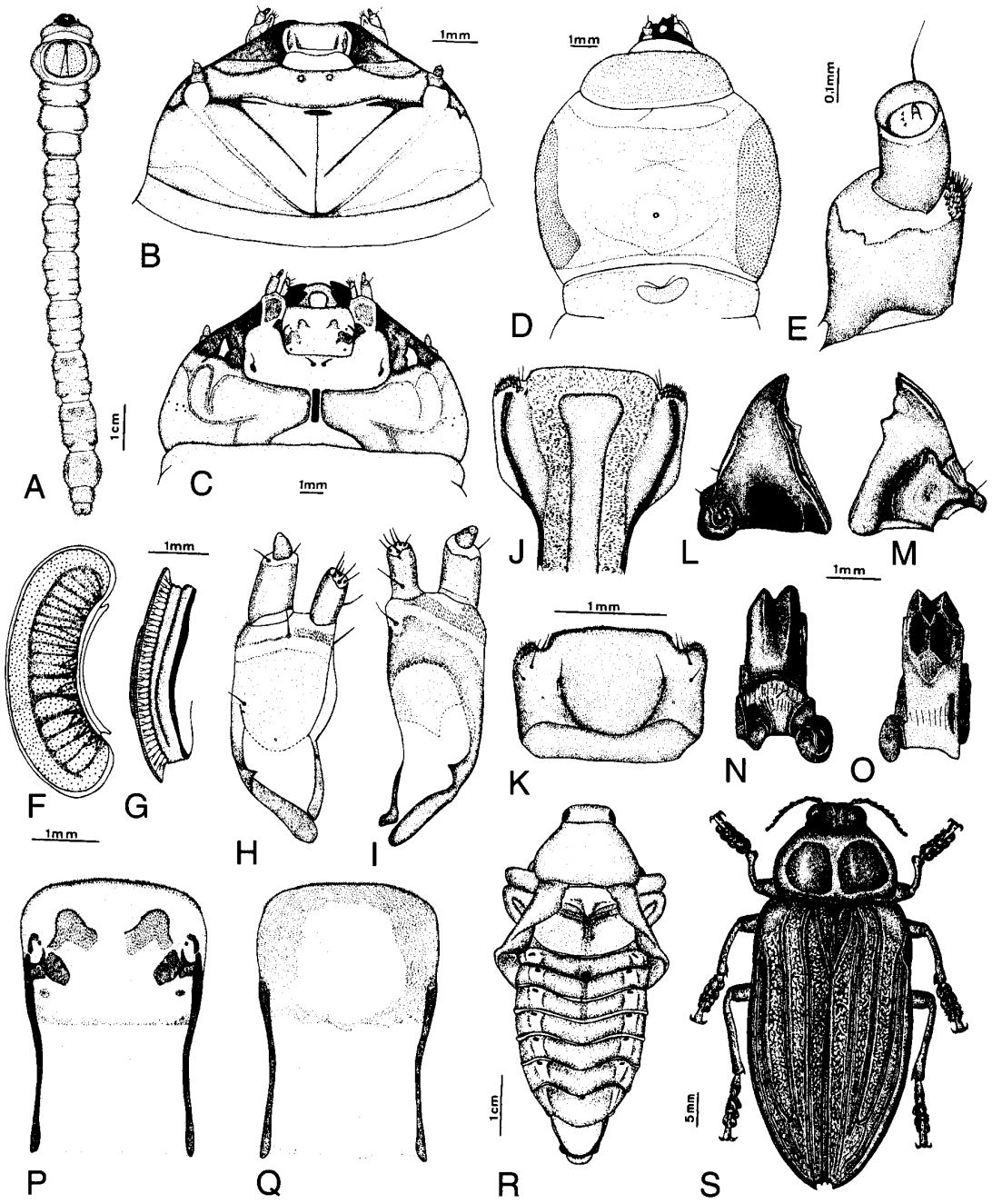

Fig. 17.1.4. *Euchroma gigantea*. A–Q, larval structures. A, habitus; B, C, head, dorsal and ventral view; D, head and prothroax, lateral view; E, antenna; F, G, spiracles, frontal and lateral; H, I, maxilla, ventral and dorsal view; J, epipharynx; K, labrum; L, M, mandible, ventral and dorsal view; N, O, mandible, lateral and mesal view; P, labium; Q, hypopharynx; R, pupa, dorsal view; S, adult. (with kind permission from Costa *et al.* 1988).

Morphology, Eggs. The eggs are sometimes relatively large, measuring 3.5 by 5 mm, belonging to Asian or African species of either *Sternocera* or *Julodis*. Gory & Laporte (1840) described and illustrated the egg and larvae of the Asian *Sternocera chrysis* F. and the larvae of four other species. The egg, larva and pupa of *Cyphosoma lawsoniae* (Chevrolat), from the Mediterranean region, were described by Bahillo & Coello (1999). Barker (1989) described the egg of the Australian *Astraeus pygmaeus* van de Poll. Otherwise, little has been reported on the eggs of this family.

Phylogeny and Taxonomy. The classification of the family is becoming better understood, although a complete modern phylogenetic perspective is lacking. Some of the genera are fairly well

known, but the classification of genera and their placement in higher taxa is still being contested. In terms of our phylogenetic understanding of the buprestids, the most recent assessment suggests that there are seven major lineages: schizopodines, julodines, polycestines, galbellines, chalcophorines, buprestines and agrilines. Some prefer that these seven groups should be placed as subfamiles of Buprestidae, but there is also compelling data to argue for familial status for one or two of these groups as well. This seven lineage concept is rather stark in contrast to the subfamily scheme proposed by Cobos (1980) where he outlined 13 subfamilies and suggested a 14th. Few attempts to use real phylogenetic analysis techniques for the family, either as a whole or for groups of taxa within, have been conducted, but these are emerging slowly and will undoubtedly increase as we try to make sense of such a large group of beetles. The last global accounting of the family came in the six buprestid parts of the Coleopterorum Catalogus by Obenberger (1926, 1930, 1934 a, 1934 b, 1936, 1937) with a summary of the higher categories provided by Bellamy (1985). The most recent higher system has been proposed by Hołyński (1993) in which he suggested four subfamilies, 12 tribes and about 64 subtribes, but many of the proposals first brought forward there are untested, or intuitively unsupportable, so further refinement is necessary. This classification was the first attempt to organize the entire family since that by Kerremans in 1893.

The system employed herein has evolved from Hołyński's scheme which has been filtered through the more empirical proposals by Volkovitsh (2001) and Volkovitsh & Bílý (2001) and summarized by Bellamy (2003).

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